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Vol. 45 No. 3

BULLETIN

OF THE

TORREY BOTANICAL CLUB

MARCH, 1918

Studies of some new cases of apogamy in ferns

W. N. Steil

(WITH PLATES 4 AND 5)

Introduction

During the past six years, the writer has made an attempt to determine to what extent under normal cultural conditions apogamy occurs in the homosporous leptosporangiate ferns and especially in the genera *Pellaea*, *Pteris*, and *Aspidium*. Since the nuclear history in only a few apogamous ferns has been investigated, it was believed that further studies in the cytology of such ferns would be desirable. Hence an investigation of this nature was undertaken in the species in which apogamy was discovered, and this part of the work has been considered more interesting and important than the discovery of new cases of apogamy. In some of the ferns studied the nuclear history is wholly or partly known, but the discussion of this subject is reserved for another paper. At this time new cases of apogamy will be reported and briefly considered.

Methods and materials

On account of the great difficulty experienced in securing spores for cultural work, the investigation, so far as the discovery of new cases of apogamy is concerned, cannot be regarded as wholly successful. Some of the spores were collected in the field. A large number of plants were grown in the university greenhouse, and

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spores were collected from these. Spores from a still larger number of species were obtained through the kindness of the following persons: Dr. A. B. Stout, New York Botanical Garden; Dr. R. C. Benedict, Brooklyn Botanic Garden; Dr. G. T. Moore, Missouri Botanical Garden; Dr. E. B. Copeland, Los Banos, Philippine Islands; Mr. F. C. Greene, Rollo, Missouri; and Rev. George Moxley, Los Angeles, California. To these gentlemen the writer wishes to express his sincerest thanks, for in no small measure they contributed to the investigation.

The spores were generally sown on the surface of a nutrient solution or on sphagnum. The latter was placed in a Stender dish and saturated with a nutrient solution. Before sowing the spores, the medium was thoroughly sterilized. Other media, such as nutrient agar, peat clay and loam, were also used, but none of these proved as satisfactory for the cultural work as the sphagnum. The Stender dishes were placed under bell-jars in a Wardian case in the university greenhouse. The jars were tilted on edge, so that the prothallia were provided with a sufficient supply of oxygen and carbon dioxid. The temperature of the Wardian case varied from 65° F. in winter to about 110° F. in summer. The prothallia were protected from too intense illumination by shading. The light was very favorable for the growth of fern prothallia since, when they were not crowded in the cultures, they became heart-shaped. The moisture supply was always sufficient for fertilization to occur in the non-apogamous species grown at the same time under precisely the same cultural conditions.

In a large number of species in which fertilization is known to occur, including *Pteris aquilina* L., *P. serrulata* L., *Osmunda regalis* L., *O. Claytoniana* L., *O. cinnamomea* L., and *Adiantum pedatum* L., sex organs were produced under the conditions just described, and embryos were formed only as a result of the union of the gametes.

The prothallia of *Nephrodium molle* Desv. and *Asplenium nidus* L., in which Yamanouchi (1908) and Nagai (1914) respectively induced apogamy, were grown under the same conditions, but while embryos were produced in large numbers, none were formed apogamously.

The spores of some of the apogamous species were sown on soil

in the university greenhouse, but the prothallia never showed any peculiarities in their development, and embryos were never produced by fertilization. Hence it appears that cultural conditions were not a factor in inducing apogamy in any case.

In the majority of cases, the prothallia were grown until embryos were formed, either as a result of fertilization or apogamously. Parthenogenesis was not excluded in the non-apogamous species. To determine this point a cytological investigation would have been necessary.

The conclusions are in no case based on a single culture but on a large number of cultures. Cultures in which only a few prothallia were obtained were always discarded. Great care was exercised in handling the spores before sowing in order to avoid, so far as possible, mixing those of different species.

Two sets of cultures were made of each of the ferns tested for apogamy. In one set only a small number of spores were sown to avoid crowding the prothallia. The prothallia under these conditions grew to a good size and became heart-shaped. It was believed that these cultures were favorable for the development of archegonia. The other cultures were made by sowing a large number of spores. The majority of the prothallia in these cultures were irregular in form and usually produced numerous antheridia. If embryos were produced, they appeared in both types of cultures. From the two sets of cultures it was possible to determine whether sex organs developed.

While the prothallia of the different species were growing, they were carefully examined from time to time with a microscope. Since in a number of species investigated tracheids appeared among the prothallial cells, it was not difficult to determine the apogamous forms. In all the apogamous species a region composed of small cells made its appearance posterior to the apical notch. In every instance when such an area of small cells appeared on the surface of the prothallium, the embryo proved to be of apogamous origin. When archegonia were produced in any of the apogamous species, they were absent on many of the prothallia. These, however, always produced embryos apogamously. In some species longitudinal sections of the prothallia were made in order to determine with more certainty the origin of the embryo.

APOGAMY IN PELLAEA AND NOTHOLAENA

The first case of apogamy in the genus *Pellaea* was discovered by Goebel (1905) in *P. nivea* (Poir.) Prantl. Later Woronin (1907, 1908) found apogamy in *P. flavens* (Sw.) C. Chr., and *P. tenera* (Gill.) Prantl., and also in *Notholaena Eckloniana* Kunze and *N. sinuata* (Lag.) Kaulf., belonging to a genus closely related to *Pellaea*. Berggren (1888), however, had already described apogamy in *N. distans* R. Br. The writer has described apogamy in *Pellaea atropurpurea* (L.) Link (Steil, 1910) and *P. adiantoides* J. Sm. (Steil, 1915*b*). New cases have since been found in *P. atropurpurea* var. *cristata* Trelease and *P. viridis* (Forksk.) Prantl.

APOGAMY IN PTERIS

Farlow (1874) discovered apogamy in *P. cretica* L. var. *albolineata* Hort. This was the first reported case in plants. Up to the present time, no other case of apogamy has been reported in any other species of *Pteris*, although Stephens and Sykes (1910) assumed that apogamy occurred in *Pteris Droogmantiana* L. Linden, on account of the presence of binucleate cells in the prothallia.

Wigand (1849) appeared to be convinced that the fern embryo did not owe its origin to fertilization. He undoubtedly described apogamous embryos, and from his descriptions and figures it is probable that he studied the development of such embryos in some species of *Pteris*. Although Wigand gives a good description of an apogamous embryo, the true nature of apogamy was first recognized by Farlow.

Tracheids were observed in the prothallium of *P. sulcata* Meyen by Leszczyc Suminski (1848). Later Mercklin (1850) confirmed the observation. Neither, however, knew the significance of the presence of such sporophytic tissue elements in the cells of the gametophyte. DeBary (1878) grew the prothallia of *P. quadriaurita* Retz. var. *argyraea* Moore but failed to find the fern apogamous.

Several years ago, without a knowledge of the observations of these investigators, the writer discovered apogamy in *P. sulcata*. Spores were obtained from the New York Botanical Garden, and

from Dr. E. B. Copeland, Los Banos, Philippine Islands. A plant obtained from Mr. Anderson, fern specialist, Short Hills, New Jersey, was grown in the university greenhouse, and spores were also collected from this plant. Archegonia were never found on any of the prothallia. However, apogamous embryos in large numbers were produced. Since numerous cultures of *P. sulcata* were made and from spores obtained from different plants, there can be no doubt that apogamy is of constant occurrence in the fern.

P. argyraea Moore has also been found by the writer to be apogamous. In many respects the prothallia and apogamous embryos are similar to those of *P. sulcata*.* In *P. Parkeri* Hort. The writer has also discovered apogamy. The prothallia become large as compared with those of the former but develop in a similar manner.

During the course of the investigation a large number of *P. cretica* varieties have been tested for apogamy, and so far none have been found which form embryos as a result of fertilization. The following is a list of these apogamous horticultural varieties: *albo-lineata Alexander*, *maxima*, *magnifica*, *Mayii*, *major*, *Wimsettii*, *Wimsettii compacta*, *Wimsettii multiceps*, *Wimsettii grandis*, and *Ouvrardi*. For the identification of some of the above varieties the writer is indebted to Mr. James C. Clark, of Philadelphia. *P. cretica* var. *albo-lineata Alexander* Hort. resembles the *P. cretica albo-lineata* in which Farlow discovered apogamy only in its second set of leaves, which are linear but with a broader band of white along the main veins of the pinnae. The first leaves are nearly all crested, while the linear leaves show sometimes a slight tendency to become crested. From the investigations which have already been made, it may be predicted that all *Pteris cretica* forms are apogamous. Apogamy has not so far been found in any of the varieties of *P. serrulata* L. f.

APOGAMY IN ASPIDIUM

Apogamy was found by De Bary (1878) in *Aspidium falcatum* (L. f.) Sw. and in a crested cultivated variety of *A. Filix-mas* (L.)

* According to Christensen (Ind. Fil. 593, 608. 1906) *P. sulcata*, *P. quadriaurita* and *P. argyraea* are all synonyms of *P. biaurita* L. According to Underwood and Benedict (Bailey's Stand. Cycl. Hort. 2852. 1916) *P. quadriaurita* is distinct from *P. biaurita*, *P. argyraea* being given as a var. *argyraea* Hort. under *P. quadriaurita*.

Sw. ("*A. Filix-mas cristatum*"). In the former Miss Allen (1911) described nuclear and cell fusions in the sporangia, previous to the formation of the spores. Kny (1895) discovered apogamy in an uncrested form of *A. Filix-mas* ("*A. Filix-mas genuinum*"). Lang (1898) found apogamy in the aberrant varieties of *A. Filix-mas*, known as "*Nephrodium pseudo-mas* var. *polydactylum* Wills" and *N. pseudo-mas* var. *polydactylum* Dadds." In these same varieties (discussed under the name "*Lastrea pseudo-mas* var. *polydactyla*"), Farmer, Moore and Digby (1903) and Farmer and Digby (1907) described remarkable nuclear fusions in the prothallium before the formation of the apogamous embryos. In a preliminary note on apospory Miss Digby (1905) had already reported apogamy in "*Lastrea pseudo-mas* var. *cristata apospora* Druery."

Heilbron (1901) found apogamy in *Aspidium aculeatum* (L.) Sw. var. *cruciato-polydactylum* Jones and *A. angulare* Willd. forma *grandidens* Moore. Five years later (Steil, 1915 *a* and *b*) apogamy was reported in *A. hirtipes* Bl. (*Nephrodium hirtipes* Hook.), *A. Tsus-Simense* Hook. and *A. chrysolobum* Kaulf. (*Lastrea chrysoloba* Presl). Apogamy has also been discovered as a result of the investigations herein described in *A. varium* (L.) Sw., *A. auriculatum* (L.) Sw., *A. caryotideum* Wallich, *Cyrtomium Fortunei* J. Sm. and *C. Rochfordianum* Hort.*

THE DEVELOPMENT OF THE PROTHALLIA AND SEX ORGANS

In all the species so far studied, the prothallia become typically heart-shaped. Between the prothallia of apogamous and non-apogamous species no difference was noted excepting that in the latter tracheids sometimes appear. The prothallia of all the species of *Aspidium* in which apogamy has been discovered bear glandular hairs on both surfaces and on the margins (PLATE 4, FIGS. 1, 2, and 5; PLATE 5, FIGS. 20 and 21), while in both *Pellaea* (PLATE 5, FIGS. 13, 14, and 15) and *Pteris* (PLATE 4, FIGS. 3, 4, and 6) such hairs are always absent. The prothallia in *Aspidium* grow to a much larger size than in *Pellaea* and in most species

* Benedict (Bailey's Stand. Cycl. Hort. 2852. 1916) gives *C. Rochfordianum* as a synonym of *C. falcatum* J. Sm. (= *A. falcatum* Sw.); Christensen (Ind. Fil. 460. 1916) includes both *A. caryotideum* and *Cyrtomium Fortunei* among the synonyms of the same species.

of *Pteris*. Those of *Aspidium chrysolobum*, *A. varium*, and *A. auriculatum* become especially large.

Antheridia are produced on the prothallia of all of the apogamous species. The antherozoids responded to the chemotactic influence of the archegonia of non-apogamous species in all cases in which tests were made. The mature antherozoid appears perfectly normal and is probably capable of functioning. In a former note (Steil, 1910) it was reported that antheridia had not been observed on the prothallia of *Pellaea atropurpurea*, but in many of my cultures made since this time they have been formed in large numbers.

Archegonia have been found on the prothallia of *Aspidium chrysolobum*, but in a large number of the prothallia they are never produced (PLATE 4, FIG. 5). The embryo always appears at the anterior portion of the cushion and can be readily observed to begin its development as a vegetative outgrowth from the prothallial cells. Over 50 per cent. of the prothallia of *Pellaea viridis* bear archegonia. Whether embryos are produced as a result of fertilization in either case has not been determined. In a few instances two embryos were observed to develop from a single prothallium of *P. viridis*. One of these was apogamously produced, but the other appeared to owe its origin to an egg. Archegonia were never found in the prothallia of *P. adiantoides*, and for this reason especial care was exercised in making the cultures of *P. viridis*. Spores were obtained from the New York and the Missouri Botanical Gardens and from two plants grown in the university greenhouse, but the embryos in all of the cultures made from the spores thus obtained were produced apogamously. In some of the *Pteris cretica* varieties archegonia were observed very rarely, but an embryo was never found to be developed from an egg.

THE DEVELOPMENT OF THE APOGAMOUS EMBRYO

The apogamous embryo usually appears as a compact region of small cells on the ventral side of the prothallium and posterior to the apical notch (PLATE 4, FIGS. 2–5, and PLATE 5, FIGS. 13 and 20). When the embryo begins its development, the prothallium has not yet attained its maximum growth. In some species, such as *Aspidium chrysolobum* (PLATE 4, FIGS. 1 and 2), *A. hir-*

tipes and *A. auriculatum*, the prothallia increase considerably in size as the young embryo is developing. In most instances the cushion has not been formed when the embryo makes its appearance. The embryo proceeds in development with the growth of the cushion. On account of the early appearance of the embryo. it was easy to determine when apogamy occurred in any species,

While the embryo usually occurs back of the apical region its position varies in the different species and even in the same species. In some cases the embryo is developed directly in the apical notch (PLATE 5, FIGS. 14 and 15). A cylindrical or conical process produced as an outgrowth of the apical region may bear on some portion of it the apogamous embryo. Sometimes the embryo may be produced at a considerable distance posterior to the notch (PLATE 5, FIGS. 13 and 20). In still other instances the embryo is formed on the lobes of the prothallium (PLATE 5, FIG. 19). From the foregoing, it is seen that the apogamous embryo can be produced on portions of the prothallia where archegonia have never been observed to be formed in any non-apogamous species.

Tracheids are visible among the prothallial cells of some of the apogamous species long before the prothallium has reached its maximum growth (PLATE 4, FIG. 3, and PLATE 5, FIG. 20).

It is usually in the portion of the prothallium where the tracheids appear that the apogamous embryo begins its development. The tracheids are readily observed in many cases, since the prothallium frequently becomes pale in the region of the notch and where these elements are produced. The cells in this portion of the prothallium contain fewer chloroplasts than the neighboring prothallial cells (PLATE 5, FIG. 20). In the species of *Pteris* the tracheids are most frequently observed (PLATE 4, FIGS. 3, 4, and 6). In many instances the light area extends forward as a cylindrical or conical process, already mentioned (PLATE 4, FIG. 6).

The embryo is usually surrounded by hairs, each composed of a single row of cells (PLATE 5, FIG. 13). In some species, as in *Aspidium chrysolobum* and *A. Tsus-Simense*, scales are also produced.

In only a few species has the development of the apogamous embryo been studied in sections. It seems that the apical cell of

the leaf always appears first, then that of the root, and finally that of the stem. A foot has never been observed to develop in any of the species in which the embryos were studied from prepared slides. Usually the leaf is much in advance of the root (PLATE 4, FIG. 9). A leaf, however, may be just making its appearance after the root has grown considerably in length (PLATE 4, FIG. 8). Both root and leaf, in the large majority of cases, are produced on the ventral side of the prothallium (PLATE 4, FIG. 7). PLATE 4, FIG. 12, represents a prothallium with an apogamous embryo the leaves and roots of which are ventral. Either root or leaf or both may appear on the dorsal surface (PLATE 4, FIGS. 10 and 11, and PLATE 5, FIG. 16). In the cultures of *Aspidium chrysolobum* and *A. hirtipes* embryos of this nature have been observed. Such anomalies may be produced by light conditions as Leitgeb (1885) has shown.

As a result of studies thus far made, it has not been determined whether the apogamous embryo owes its origin to a single superficial cell or to inner and outer cells of the prothallium.

Frequently, in some of the cultures, more than one embryo was observed to develop from a single prothallium. This was especially the case when the prothallia showed a tendency to become lobed (PLATE 4, FIGS. 3 and 4). PLATE 4, FIG. 3, represents a prothallium of *Pteris cretica albo-lineata Alexander* with a young embryo posterior to the apical region, and tracheids in each of the two secondary regions of growth. Another prothallium of the same variety is shown in PLATE 4, FIG. 4. In this instance tracheids are present in the apical region, and two embryos have been produced on other portions of the prothallium. One of these is produced in the apical region of one of the main lobes, and the other is a vegetative growth on the inner margin of a lobe itself. Each of these embryos has produced a small leaf, *l*, and a root, *r*. The embryos in such cases, as is readily seen, are wholly independent of one another. In some instances it was observed that some of the tracheids extended from the apical notch of the prothallium to one or both of the inner margins of the lobes where the embryo was produced (PLATE 5, FIG. 19). It may be stated in this connection that embryos are not always produced when tracheids are formed, but in most cases these tissue-elements indicate the beginning of an apogamous embryo.

In one of the cultures of *Pteris sulcata*, conical and nearly spherical projections were observed in the lobes of the prothallia. Some of these prothallia were transferred to another culture, and the growth of the projections was followed in both cultures. The projections produced either secondary prothallia or apogamous embryos. The former were often cylindrical at the point of origin, but in other respects they resembled the ordinary prothallia of *Pteris sulcata*. As many as six embryos were observed on the lobes of a single prothallium. In most instances these were normal, producing both roots and leaves.

By cultural conditions secondary prothallia have been produced from the primary prothallia of many of the apogamous species. These prothallia also form embryos apogamously. DeBary (1878) reported that such prothallia of *Pteris cretica albo-lineata* seldom produced embryos. However, in my cultures of the same species, the secondary prothallia usually produced embryos of apogamous origin. Secondary prothallia of *Pellaea atropurpurea*, *Aspidium hirtipes*, *Pteris sulcata*, *Pteris argyraea*, and *Pteris cretica albo-lineata Alexander* frequently produce apogamous embryos.

THE INFLUENCE OF WEAK ILLUMINATION ON THE DEVELOPMENT OF THE PROTHALLIA AND OF THE APOGAMOUS EMBRYOS

When the prothallia of the apogamous species were placed under the influence of weak light, the same results were obtained as with the non-apogamous ferns. Filaments were formed from the margin and both surfaces of the prothallia (PLATE 5, FIG. 21), and these under the normal conditions of illumination in the wardian case became independent prothallia, which in nearly all instances formed also apogamous embryos. When the prothallia were maintained in weak light, they remained simple or branched filaments, producing neither sex-organs nor embryos (PLATE 5, FIG. 18). Under somewhat more favorable conditions of illumination, ribbon-like plates were produced, which frequently bore numerous antheridia and occasionally apogamous embryos. When the illumination was slightly less than that in the greenhouse, the prothallia became lobed (PLATE 5, FIGS. 14 and 15). In the new apical regions which were formed embryos also made their appearance (PLATE 5, FIG. 17).

The conical or cylindrical processes already described grew considerably in length when the cultures were placed in weak light. In such instances an apical cell could be readily distinguished. The embryo in these cultures was frequently formed on the process, and usually it was produced as a direct outgrowth of the apical notch. The "light" area, or pale portion of the prothallium where the embryo begins its development, remains more conspicuous under these conditions. The colorless plastids, present in large numbers in the cells of the pale region, become chloroplasts under favorable conditions of light, and hence the nearly colorless region is not so clearly differentiated in the latter case.

ATTEMPT TO INDUCE APOGAMY IN OSMUNDA REGALIS

In the latter part of July, 1912, a large number of prothallia of *Osmunda regalis* were found by the writer in a swamp in the vicinity of Madison. Most of the prothallia at this time were small but had produced numerous antheridia. Some of the prothallia were removed with a depth of about three inches of soil and placed under bell jars in the university greenhouse. Several cultures were kept in a Wardian case where the illumination was very favorable for the normal development of the prothallia. Other prothallia were placed under bell jars and in different parts of the greenhouse where strong light was obtained for the greater part of the year. The latter were watered only from below and great care was exercised to prevent condensation of moisture on the prothallia. In this manner fertilization was prevented for nearly a year and a half. During this period, however, the prothallia grew to a large size, and numerous antheridia and archegonia were produced. Many of the prothallia reached a length of three centimeters. On such prothallia most of the archegonia were formed in acropetal succession, but frequently a number were produced among the older archegonia. In one instance the archegonia on one side of the "midrib" of a prothallium, measuring two centimeters in length, were counted and approximately five hundred were found to be present. Therefore this prothallium had produced about one thousand archegonia.

When the prothallia were freely watered, embryos were pro-

duced in large numbers as a result of fertilization. Hence it is certain that the cultural conditions which were maintained rendered fertilization impossible. The prothallia grown under favorable conditions were smaller, but produced numerous sex organs and embryos only as a result of fertilization.

Since the prothallia for the cultural work were found growing under plants of *Osmunda regalis*, and since no other osmundas were growing in the immediate vicinity, it could hardly be assumed that the prothallia could be referred to any other species. Nevertheless, spores of *O. regalis* were collected and sown in the Wardian case, and in every respect the prothallia grown corresponded to those brought from the field.

The experimental work with *Osmunda regalis* was of especial interest, since Leitgeb (1885) reported in this species the occasional occurrence of apogamy. No one, however, has confirmed the observation. Although Lang (1898), Yamanouchi (1908), Pace (1913), and Nagai (1914) believed that apogamy might be brought about by cultural conditions, Miss Black (1909) and Mottier (1915) were unable to produce a single apogamous embryo by cultural conditions.

SUMMARY

1. The prothallia of a number of species of ferns in which apogamy was discovered were grown under cultural conditions favorable for the development of sex-organs and embryos in non-apogamous species.

2. The prothallia of all the apogamous ferns become heart-shaped before the formation of the embryo. Antheridia are produced on the prothallia of all apogamous forms, but archegonia are formed on the prothallia of only a few forms.

3. The embryo usually appears as a compact region of cells posterior to the apical notch and on the ventral side of the prothallium. In a number of species tracheids are visible among the prothallial cells in the pale portion of the gametophyte.

4. First to make its appearance is the apical cell of the leaf, then that of the root, and later that of the stem. A foot has not, so far, been observed to develop in connection with the apogamous embryos.

5. Either root or leaf or both of these organs may develop on the dorsal side of the prothallium. As a rule, however, they are produced on the ventral side.

6. While the embryo is produced as a rule posterior to the apical notch, it may be formed on a cylindrical or conical "process" and in some instances on the lobes of the prothallium.

7. Several apogamous embryos may be formed on a single prothallium.

8. As in non-apogamous species, secondary prothallia are readily produced, and these form embryos like those of the ordinary prothallia.

9. The "light" area present on the prothallium of some of the apogamous species is rendered more conspicuous in cultures maintained in weak light. The conical or cylindrical "process" increases considerably in length when the prothallia are grown under these conditions. As a result of weak illumination, the embryo is frequently produced as a direct outgrowth of the apical region of the prothallium.

10. By growing the prothallia of *Osmunda regalis* in strong light and preventing fertilization for a year and a half, no embryos were produced apogamously.

11. An investigation extending over a period of six years has resulted in the discovery of apogamy in a large number of ferns. The conclusion that apogamy is of frequent occurrence in the genera *Pellaea*, *Pteris*, and *Aspidium*, is justified on the basis of the many cases so far found in these genera.

I wish to thank Professor C. E. Allen for suggestions and criticisms received during the progress of the foregoing investigation.

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Description of plates 4 and 5

The photomicrographs of the prothallia on PLATE 4, and FIGS. 13, 14, 15, and 18 on PLATE 5, represent a magnification of about twenty diameters. FIGS. 19, 20, and 21 on PLATE 5 show a much higher magnification. The apogamously produced sporophytes were magnified about two and one half times. All the figures were reduced one seventh in reproduction.

PLATE 4

FIG. 1. A ventral view of a prothallium of *Aspidium chrysolobum* just before the beginning of the apogamous embryo.

FIG. 2. A similar view of a prothallium of the same species. The apogamous embryo is represented as a black region posterior to a pale region in the apical portion of the prothallium.

FIG. 3. A ventral view of a prothallium of *Pteris cretica albo-lineata Alexander*. In the apical region a young embryo is developing. In the apical regions established in the lobes tracheids are present.

FIG. 4. A ventral view of a prothallium of *Pteris cretica albo-lineata Alexander*. An embryo with root and leaf has been produced in the new apical region of one of the lobes. On the inner margin of the other lobe a young embryo has also appeared. In the main apical region tracheids are visible.

FIG. 5. A dorsal view of a prothallium of *Aspidium chrysolobum*. The prothallium produced no archegonia. The apogamous embryo appears as a dark region posterior to the apical notch.

FIG. 6. A prothallium of *Pteris cretica albo-lineata*. A tongue-like portion has developed as an outgrowth of the apical region. In the larger secondary prothallium the "pale" region has already appeared.

FIG. 7. A ventral view of a prothallium of *Aspidium hirtipes* with an embryo whose root and leaf are produced on the ventral surface.

FIG. 8. An embryo of *A. hirtipes* with a well-developed root.

FIG. 9. An embryo of *A. hirtipes* with only the leaf well developed.

FIG. 10. An embryo of *A. chrysolobum*, one root of which is on the dorsal surface, and the other on the ventral.

FIG. 11. An embryo of *A. chrysolobum* whose root is on the dorsal surface and leaf on the ventral surface.

FIG. 12. A young sporophyte of *A. hirtipes* with three primary leaves and a single ventral primary root.

PLATE 5

FIG. 13. A ventral view of a prothallium of *Pellaea adiantoides*. The young embryo is surrounded by hairs.

FIG. 14. A prothallium of *Pellaea adiantoides* grown in slightly weaker illumination than that maintained in the Wardian case. The prothallium has become distinctly lobed, and the embryo is developed in the apical region.

FIG. 15. A similar prothallium of the same species. The lobes are still more conspicuous and the embryo has grown to a larger size.

FIG. 16. An embryo of *Aspidium chrysolobum*, one leaf of which is on the dorsal surface and the other on the ventral surface of the prothallium. The long root is also on the ventral surface.

FIG. 17. A portion of a lobed prothallium of *A. hirtipes* bearing two embryos, each of which has a well-developed leaf and root.

FIG. 18. Filaments of a single row of cells of prothallia of *A. hirtipes* grown in weak illumination.

FIG. 19. A prothallium of *Pteris sulcata*, showing the beginning of an embryo in the apical notch. Tracheids pass upward to the young embryo, which has been produced on the inner margin of a lobe.

FIG. 20. An embryo of *A. hirtipes* beginning its development in the apical region. The "pale" region and tracheids are clearly differentiated.

FIG. 21. Secondary prothallia of *A. hirtipes* produced from the margins and surfaces of a prothallium placed in weak light.

Correlation of morphological variations in the seedling of Phaseolus vulgaris

J. Arthur Harris and B. T. Avery

Introductory remarks

During the past several years one of us has had under way extensive experiments on the differential death-rate of bean seedlings. Individuals differing in structure also differ in their capacity for survival under field conditions,* and in such physiological characteristics as capacity for the development of the tissues of the primordial† and of the subsequent leaves.‡

Some tens of thousands of seedlings of known morphological characteristics have been exposed to risk, as the life insurance statisticians express it, in an attempt to determine the selective value of the various morphological variations. These seedlings were, for technical reasons, necessarily planted in the field at a time when the cotyledonary node and the primordial node only could be studied. It is evident that the capacity of the plant for survival may be in some degree dependent upon characters developed later in ontogenesis, but correlated with characters of the first or second node of the seedling.

However this may be, it is certainly true that a full knowledge of the morphology and physiology of the variant bean seedling demands a thoroughgoing investigation of the correlation between the structure of the first two leaf whorls and that of later whorls. We have, therefore, been forced to consider the problem of the morphological character of the leaf whorls produced at the third

* Harris, J. Arthur. A simple demonstration of the action of natural selection. Science II. **36**: 713–715. 1912.

† Harris, J. Arthur. Studies on the correlation of morphological and physiological characters: the development of the primordial leaves in teratological bean seedlings. Genetics **1**: 185–196. 1916.

‡ Harris, J. Arthur. Further studies on the interrelationship of morphological and physiological characters in seedlings of *Phaseolus*. Mem. Brooklyn Bot. Gard. **1**. *In press.*

node in the case of plants showing various structural abnormalities at the first two nodes.

Phaseolus is well suited for such investigations. The normal seedling has two cotyledons, inserted at the same level, and two opposite primordial leaves. A large number of structural variations, four types of which will be considered in this paper, may occur. The chief disadvantage lies in the rarity of many of the variations in the lines with which we have dealt. The securing of adequate series is excessively laborious. The present paper is based upon a careful study of the variations in the first three nodes of 16,348 plants, which were selected from about 450,000 seedlings examined for the characters of the first and second node.

When in the following paragraphs we refer to normal and abnormal plants or seedlings, it must be understood that this applies to the characteristics of the individual as determined on the basis of the first two nodes, the cotyledonary and the primordial only. In its later development the "abnormal" plant may remain "abnormal" or become "normal," and the "normal" plant may either continue to be "normal" or become "abnormal."

The nature and method of classification of the abnormalities dealt with will be discussed in the presentation of the data below.

MATERIALS AND METHODS

The materials upon which this study is based are a series of lines of White Navy beans grown at the Station for Experimental Evolution during the past several years. The seeds were harvested from field cultures in 1915 and germinated in sand in the autumn of 1916.

Seedlings which were abnormal in the characters of the first or second node, i. e., in the number or insertion of the cotyledons or of the primordial leaves, were sorted out for potting in soil and subsequent study of the third node, that normally giving rise to the first compound leaf.

For each abnormal individual, a normal control seedling from the same parent plant was taken at random to serve as a basis of comparison. Both were potted in soil and grown to a stage when the characteristics of the third node could be accurately determined.

For the onerous preliminary examination of nearly a half a million seedlings we are greatly indebted to Miss Edna K. Lockwood, Miss Margaret Gavin and especially to Miss Lillie Gavin.

PRESENTATION AND ANALYSIS OF DATA

The slightest abnormality which we have been able to discover occurring in considerable numbers of bean seedlings is the vertical separation of the two normally opposite cotyledons. So imperceptible is the line of transition between normal and abnormal that personal equation must play some part in classification. The cotyledons may be much more widely separated. The variation is a purely graduated one, with no sharp lines of demarcation between the different degrees of separation. Generally we have recognized three grades, but because of the rarity of plants with more widely separated cotyledons we have in this paper grouped our data into two classes only. The first comprises plants with cotyledons 2–3 mm. apart. The second includes all those in which they are more distant.

The number as well as the position of the cotyledons may vary. Plants with three instead of two cotyledons fall into two groups; those with the normal pair of primordial leaves and those with a whorl of three leaves. The latter are by far the more abundant.

Abnormality developed subsequently to the selection of the seedlings in the preliminary sorting may affect either the internode between the second and the third nodes, that is, between the primordial leaf whorl and the point of insertion of the first compound leaf or leaf whorl, or it may be confined to the number or structure (or number and structure) of the leaves inserted at the third node.

In the original selection of individuals abnormal in the characters of the first or second node, only those with sensibly normal axes (hypocotyl and epicotyl) were chosen for the purposes of the present study.

Two types of abnormality in the axis beyond the second (the primordial) node have been considered.

The first is a sensible broadening of the axis, identical with or similar to fasciation. This is a graduated character. The line of demarcation between normal and abnormal is not clearly marked.

and personal equation may influence in some degree the classification of the seedlings.

The second is a division of the axis into two coördinate branches each with a terminal bud.

The frequencies of the two types of axial variation are too small to justify detailed discussion. The entries in TABLE I show that

TABLE I

FREQUENCIES OF ABNORMALITY OF SECOND INTERNODE IN NORMAL AND ABNORMAL SEEDLINGS

Class of abnormality	Actual frequencies			Percentage frequencies		
	Normal internode	Broadened internode	Divided internode	Normal internode	Broadened internode	Divided internode
Two cotyledons slightly separated; two primordial leaves	4,017	5	8	99.6774	.1240	.1985
Normal control	4,029	0	1	99.9751	.....	.0248
Difference	−12	+ 5	+ 7	−.2977	+ .1240	+.1737
Two cotyledons widely separated; two primordial leaves	878	2	1	99.6594	.2270	.1135
Normal control	881	0	0	100.0000	.....	.....
Difference	−3	+ 2	+ 1	− .3406	+ .2270	+.1135
Three cotyledons; two primordial leaves	813	12	0	98.5454	1.4546	.....
Normal control	825	0	0	100.0000	.....	.....
Difference	−12	+12	0	−1.4546	+1.4546	.....
Three cotyledons; three primordial leaves	2,410	14	14	98.8515	.5742	.5742
Normal control	2,436	2	0	99.9179	.0820	.....
Difference	−26	+12	+14	−1.0664	+ .4922	+.5742

in every instance in which any individuals at all are available the seedlings which are abnormal in either the cotyledonary or the primordial node show a higher percentage of abnormality in the structure of the internode beyond the second node than do the normal controls.

We now turn to a consideration of variation in the leaves inserted at the third node. The leaves of plants with abnormality of the axis should not be combined with those having normal axes. They are not sufficiently numerous for separate consideration.

Confining our attention to seedlings which have a normal axis for at least the length of the second internode of the epicotyl, we

have the frequencies shown in TABLES II–V.* The character of the control plants is also given.

TABLE II

SEEDLINGS WITH TWO COTYLEDONS SLIGHTLY SEPARATED AND TWO PRIMORDIAL LEAVES

Number of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	3,791	3,853	94.37	95.63	−1.26
2	225	176	5.60	4.37	+1.23
3	1	0	.02	.00	+ .02
Totals.....	4,017	4,029	99.99	100.00	

TABLE III

SEEDLINGS WITH TWO COTYLEDONS WIDELY SEPARATED AND TWO PRIMORDIAL LEAVES

Number of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	811	840	92.37	95.35	−2.98
2	67	41	7.63	4.65	+2.98
Totals.....	878	881	100.00	100.00	

TABLE IV

SEEDLINGS WITH THREE COTYLEDONS AND TWO PRIMORDIAL LEAVES

Numbes of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	591	792	72.69	96.00	−23.31
2	221	33	27.18	4.00	+23.18
3	1	0	.12	.00	+ .12
Totals.....	813	825	99.99	100.00	

TABLE V

SEEDLINGS WITH THREE COTYLEDONS AND THREE PRIMORDIAL LEAVES

Number of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	1,632	2,200	67.72	90.31	−22.59
2	771	236	31.99	9.69	+22.30
3	7	0	.29	.00	+ .29
Totals.....	2,410	2,436	100.00	100.00	.....

* In these tables the numbers of control plants are not exactly identical with the numbers of abnormal plants, since some of those selected as normal in the seedling stage showed abnormality of the axis in subsequent development and are omitted here, where we are discussing abnormalities of foliar characters only.

In each of the types of abnormality dealt with the abnormal series show a higher proportion of the individuals with two or three leaves at the third node than do their normal controls.

Furthermore, seedlings showing different types of abnormality at the first nodes also differ among themselves in the extent of abnormality at the third node. Thus plants which are normal except for slight separation of the cotyledons have two or three leaves at the second node instead of the single leaf normally found in 5.63 per cent. of the individuals. Plants with the cotyledons more widely separated have 7.63 per cent. of their number with two or three instead of a single leaf.

When one turns to the groups of plants which have three instead of two cotyledons, a conspicuous difference is at once apparent. Plants which have three cotyledons and a normal pair of primordial leaves produce two or three instead of a single leaf at the third node in 27.31 per cent. of the cases. Seedlings with three cotyledons and a whorl of three primordial leaves instead of the normal pair at the third node have 32.29 per cent. of the individuals with two or three leaves at the third node.

Heretofore the number of leaves inserted at the third node has furnished the only measure of variation at this region of the axis. We now propose to consider variation in the organization of the leaves themselves. It will not be possible to do this in the detail in which we hope to treat the problem ultimately. The range of variation in the division of the bean leaf is rather great, and the laws governing it are doubtless very complicated. Some progress has already been made on the problem, but for the present we shall limit our discussion to the number of leaflets, leaving the problem of their arrangement for treatment when even larger series of data are at our disposal.

The actual frequencies of number of leaflets per leaf produced at the third node are shown in TABLE VI.

The most conspicuous feature of this table is the bimodal nature of the distribution. The modes are on three and six, as is to be expected from the fact that the distribution of the whole number of leaflets depends upon plants with from one to three leaves at the third node.

Because of the wide range of variation in leaflet number it is

not feasible to reduce these frequencies for the individual classes to a percentage basis for comparisons. This has, however, been done for larger groups secured by combining all the seedlings

TABLE VI

NUMBER OF LEAFLETS PRODUCED AT THE THIRD NODE BY SEEDLINGS OF VARIOUS TYPES

Number of leaflets	Two cotyledons slightly separated and two primordial leaves		Two cotyledons widely separated and two primordial leaves		Three cotyledons and two primordial leaves		Three cotyledons and three primordial leaves	
	Abnormal	Control	Abnormal	Control	Abnormal	Control	Abnormal	Control
1	5	2	1	...	1	...	....	....
2	16	6	4	...	3	2	2	5
3	3,741	3,825	801	835	572	782	1,602	2,185
4	27	21	5	4	14	5	28	8
5	10	2	1	2	6	3	9	2
6	215	173	65	40	203	33	751	236
7	1	....	1	...	12	...	12	....
8	....	....	...	...	1	...	....	....
9	1	....	...	...	1	...	3	....
10	1	....	...	...	...	...	2	....
11	....	....	...	...	...	...	1	....
Totals	4,017	4,029	878	881	813	825	2,410	2,436

showing merely separation of the cotyledons and all those showing three cotyledons instead of the normal two. The results are shown in the accompanying TABLE VII, which is self explanatory.

TABLE VII

COMPARISON OF THE NUMBER OF LEAFLETS IN DICOTYLEDONOUS AND TRICOTYLEDONOUS SEEDLINGS WITH THAT IN THEIR NORMAL CONTROLS

Number of leaflets	Seedlings with cotyledons separated		Seedlings with three cotyledons	
	Abnormal	Control	Abnormal	Control
1	.12	.04	.03	....
2	.41	.12	.16	.21
3	92.79	94.91	67.45	90.98
4	.65	.51	1.30	.40
5	.22	.08	.47	.15
6	5.72	3.52	29.60	8.25
7	.04	.81	.74	....
8	....	....	.03	....
9	.02	....	.12	....
10	.02	....	.06	....
11	....	....	.03	....

A comparison may be made without the combination of different grades of abnormality by grouping the number of leaflets

around the modal classes 3, 6 and 9. The results in TABLE VIII show essentially the same relationships as those given in TABLES VI–VII. First, the higher leaflet numbers are more extensively represented in the abnormal plants of each of the four types than they are in the controls. Second, the tricotyledonous plants show a far greater increase in the number of leaflets inserted at the third node than do those abnormal only in the position at which the two cotyledons are inserted.

TABLE VIII

PERCENTAGE FREQUENCIES OF NUMBERS OF LEAFLETS IN SEEDLINGS OF VARIOUS TYPES

Class of abnormality	Number of leaflets		
	1–4	5–7	8–11
Two cotyledons slightly separated and two primordial leaves	94.32	5.62	.05
Control	95.66	4.34	....
Difference	− 1.34	+ 1.28	+.05
Two cotyledons widely separated and two primordial leaves	92.37	7.63	....
Control	95.23	4.77	....
Difference	− 2.86	+ 2.86	....
Three cotyledons and two primordial leaves	72.57	27.18	.24
Control	95.64	4.36	....
Difference	−23.07	+22.82	+.24
Three cotyledons and three primordial leaves	67.72	32.03	.25
Control	90.23	9.77	....
Difference	−22.51	+22.26	+.25

In substantiation of these conclusions the reader will note that in the class with slightly separated cotyledons 5.68 per cent. of the plants have from five to ten leaflets as compared with 4.34 per cent. with five and six leaflets in the control series. In seedlings with more widely separated cotyledons but no other abnormality there are 7.63 per cent. of the plants with five to seven leaflets as compared with 4.77 per cent. of the normal controls with five or six leaflets. Seedlings with three cotyledons but the normal number of primordial leaves have 27.43 per cent. of the individuals with from five to nine leaflets as compared with 4.36 per cent. with five or six leaflets in the normal controls.

Plants with a trimerous cotyledonary and primordial whorl have 32.28 per cent. of the seedlings with from five to eleven leaflets

as compared with 9.77 per cent. with five and six leaflets in the normal controls.

Taking the average number of leaflets per plant as a basis of comparison between the abnormal plants and their controls we find the results in TABLE IX.

TABLE IX

MEAN NUMBER OF LEAFLETS IN SEEDLINGS OF VARIOUS TYPES

Class of abnormality	Mean number of leaflets in abnormals	Mean number of leaflets in controls	Difference
Two cotyledons slightly separated; two primordial leaves	3.170	3.133	+0.037
Two cotyledons widely separated; two primordial leaves	3.228	3.191	+0.037
Three cotyledons; two primordial leaves	3.847	3.131	+0.716
Three cotyledons; three primordial leaves	3.990	3.294	+0.606

Note (*a*) that for each type of normality the average number of leaflets is greater in the abnormal individuals than in the normal, and (*b*) that the difference between the abnormal class and its control is far greater in the case of the plants with three cotyledons than in those in which the abnormality in the cotyledonary whorl consists merely in the separation of the two cotyledons.

Thus the results for number of leaflets substantiates the conclusion based upon number of leaves.

Evidently, however, the number of leaflets is to a great extent determined by the number of leaves. The problem now arises: Are there differences in the average number of leaflets per leaf in the abnormal and normal individuals?

Means and their differences have been determined, but are so slight that conclusions must be deferred until further series of data are available.

Just one other method of dealing with the problem of the correlation in structural variation may now be considered.

Number of leaflets is, in the materials dealt with, practically an integral variate. In examining a large series of plants those with partial division of a leaflet, representing transition stages between a leaf with n and one with $n + 1$ leaflets are sometimes found. Such cases are, however, relatively rare. The lobing of the leaflet has therefore been disregarded in the foregoing treat-

ment. A leaf with three leaflets, one of which has a lobe, has been recorded as 3 in the tables, not as an intermediate between three and four. This has simplified the tabling of the data, and the calculation of the simple constants necessary to the interpretation the data, without any material loss in accuracy.

One may, however, inquire whether there are differences in the degree of lobing of the leaflets produced at the third node in plants which are normal and in plants which are abnormal in the characters of the first and second node. Because of the very low percentages of lobing in the leaflet no stress whatever is to be laid upon the exact values found, even in samples containing several hundreds or thousands of plants, because of the great difficulties of determining the probable error of a small percentage.

The results are given in TABLE X.

TABLE X

PERCENTAGE OF LOBING IN THE LEAVES OF SEEDLINGS OF VARIOUS TYPES

Class of abnormality	Abnormal plants	Control plants	Difference
Two cotyledons slightly separated; two primordial leaves	0.349	0.273	+0.076
Two cotyledons widely separated; two primordial leaves	0.456	0.112	+0.344
Three cotyledons; two primordial leaves	1.599	0.242	+1.357
Three cotyledons; three primordial leaves	0.954	0.328	+0.626

Here the percentage frequency of plants with one or two lobes on the leaflets* are given for each type of abnormality dealt with and compared with that found in the control series.

Two relationships seem clearly indicated by the constants in this table.

First, the tendency to the production of lobes is greater in the leaflets produced by abnormal plants of all four types than in their normal controls.

Second, the tendency to the production of lobes is greater in the leaflets of plants with a trimerous cotyledonary whorl, and either a dimerous or trimerous primordial whorl, than it is in plants in which the sole abnormality consists in the separation of the two cotyledons in their insertion on the axis of the plant.

* In the case of two lobes both may occur on the same leaflet or they may be on different leaflets.

RECAPITULATION

This paper presents the results of a first attempt to determine some of the correlations in the structural variations of the seedling of *Phaseolus vulgaris*.

The materials are drawn from a series of lines of Navy beans grown for the past several years at the Station for Experimental Evolution. The seeds used were harvested from plants of selected ancestry. Neither of these factors will, we believe, invalidate the conclusions drawn in this paper. These conclusions will not necessarily apply to certain entirely abnormal races.

Fasciation-like broadening of the axis and longitudinal division of the axis distal to the insertion of the primordial leaves are both more frequent in seedlings showing separation of the cotyledons and in tricotyledonous seedlings than in those which are normal.

Seedlings which are normal except for the separation of the cotyledons and those which have three cotyledons and a normal pair of primordial leaves or three cotyledons and a whorl of three primordial leaves produce a larger number of leaves, a larger number of leaflets and a higher percentage of leaves with lobes at the third node than do those which are normal in their cotyledonary and primordial leaf characters.

Seedlings which are tricotyledonous, with either a normal pair or a whorl of three primordial leaves, show higher percentages of variation in the axis, or the leaves produced by the axis, distal to the primordial leaves than do those which are normal except for the separation of the two cotyledons.

These studies will be continued.

STATION FOR EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, NEW YORK

INDEX TO AMERICAN BOTANICAL LITERATURE

1913-1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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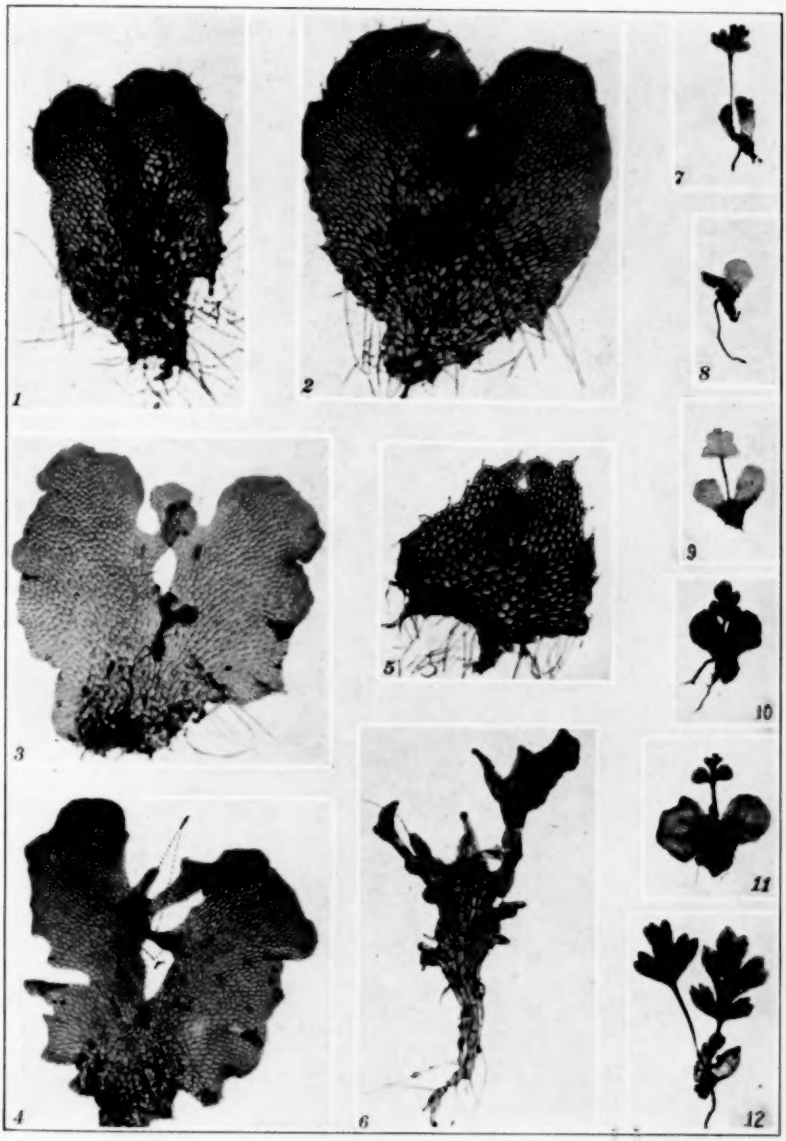

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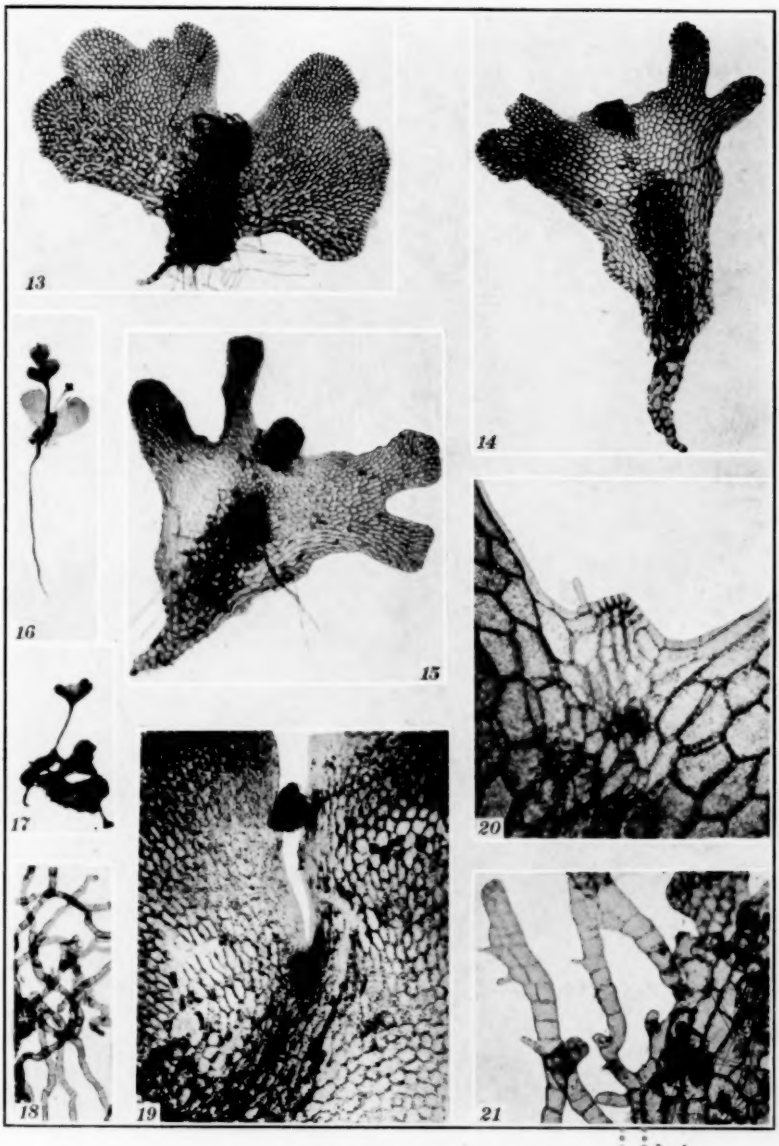

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